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STRUCTURE AND DYNAMICS OF COMMUNAL GROUPS IN THE BEECHEY JAY

Ralph J. Raitt, Scott R. Winterstein, and John William Hardy

Studies of avian cooperative breeding now have progressed to the stage at which attempts have been made to formulate generalizations concerning its adaptive significance and mode of evolution (Brown 1969, 1974, 1978, 1980, 1982, 1983, in press; Ricklefs 1975; Fry 1977; Emlen 1978, 1982a, b; Gaston 1978; Koenig and Pitelka 1981; Ligon 1983). Prominent among the studies contributing to the success of those who attempt generalization are several on New World jays, including especially those of Brown (1963, 1970, 1972; Brown and Brown 1980, 1981a) on the Mexican or Gray-breasted Jay (*Aphelocoma ultramarina*) and of Woolfenden (1973, 1975, 1978, 1981; Woolfenden and Fitzpatrick 1977, 1978; Stallcup and Woolfenden 1978) on the Florida Scrub Jay (*A. c. coerulescens*).

The black-and-blue jays of the subgenus *Cissilopha,* genus *Cyanocorax,* are a group of several allopatric forms of Mexico and Central America, all of which breed cooperatively (Hardy 1976; Raitt and Hardy 1976, 1979; Hardy et al. 1981). In a comparative study of the behavior and ecology of this group we gave particular attention to the relationships of population structure and dynamics to cooperative breeding in the Beechey Jay (*Cyanocorax beecheii*), the northernmost of the forms and apparently the only one in which some breeding pairs regularly have helpers and others do not.

We studied a population of *C. beecheii* from 1974–1978 near Mazatlan, Sinaloa, Mexico. As described in an earlier paper (Raitt and Hardy 1979) and confirmed by the findings of an additional two years of study (1977–1978), these jays occupy dense, lowland deciduous forest, in a highly seasonal climate with a continuous very dry period that lasts about 6 months. They live throughout the year in groups of 2–6 fully grown birds (yearlings or older), on large territories (25–43 ha) that they defend against members of other groups. Parenthood within a group is confined to a single adult (≥ 3 years old) member of each sex. No more than one successful nesting attempt is made by a breeding pair each year; renesting was observed only after failure of a first attempt. All members of a group help to defend the nest and to feed nestlings and probably all participate to some degree in nest construction and care of fledglings. We ascribe the relatively large body size, large territory, and relatively low reproductive output in this species to relatively low productivity of food in a seasonally severe and generally dry climate (Raitt and Hardy 1979).

We examined various hypotheses that form the core of developing theory concerning the evolution and adaptive significance of cooperative breeding in birds. These include advantages and disadvantages of helping to both helpers and breeders, genetic relatedness within breeding groups, age of helpers and breeders, the mode by which helpers attain breeding status, and other aspects of cooperative breeding.

METHODS

We captured and marked jays with distinctive combinations of colored leg bands and plastic flags (see Raitt and Hardy 1976). Ninety-six birds were marked, the majority ($N = 63$) as nestlings. It was difficult to capture fully grown birds and a few remained unmarked. The stability of group composition, obvious morphological age variation, and the small number of unmarked individuals per group (usually no more than one) permitted most of the latter to be individually identifiable.

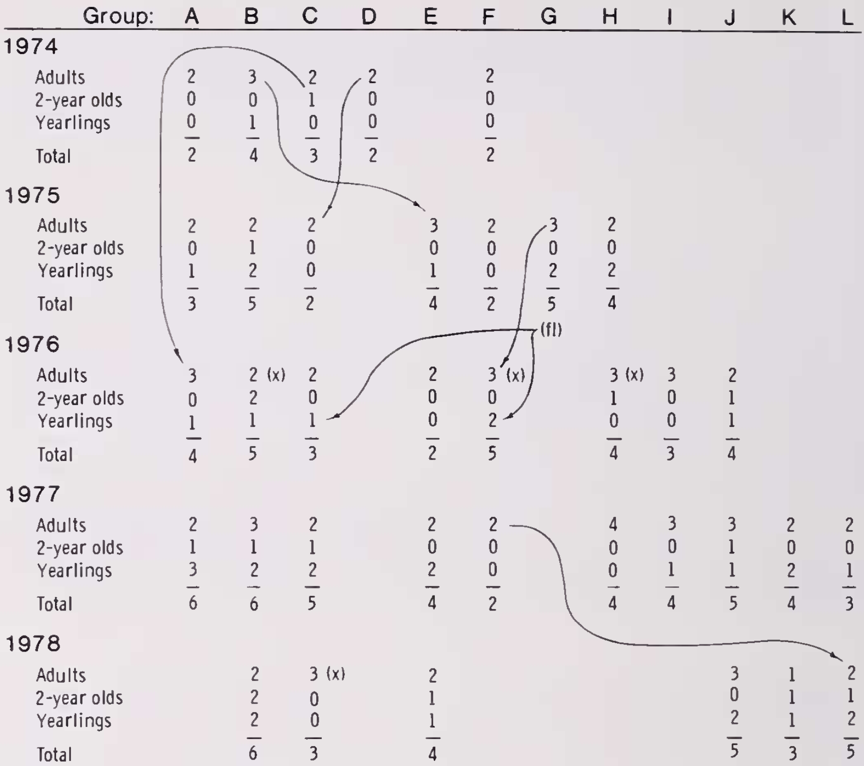
We observed the jays' activities, including movements; located as many nests as possible; followed progress of nests; and observed activity at and around them. In conducting timed observations of activity at nests, we sampled opportunistically, but at all nests we made as many observations as possible at different times of day in each stage of the nest cycle. Nests of nearly all known groups in each year were found and fates of nesting efforts determined; a small number of late, second attempts were still in progress on termination of our field work for the respective summers.

RESULTS

Group composition and stability.—As indicated in the earlier paper, each breeding-season group included at least one adult member of each sex; some consisted only of such a pair but most also included helpers (Fig. 1, Appendix). Helpers included individuals of all three major age classes of fully grown birds: yearlings, 2-year-olds, and adults. An apparent year-to-year trend of increasing size of groups is not statistically demonstrable by Chi-square test ($\chi^2 = 12.24$, df $= 16$, $P > 0.5$).

Several of the groups, most of which had a considerable degree of continuity of individual membership, occupied the same territory year after year (e.g., groups A, B, E, Fig. 1). Some groups, however, dissolved. Destruction of habitat was implicated in the dissolution of groups A and F; D and G disintegrated and H and I simply disappeared, all without severe habitat disturbance. In D and G one member of the previous year's breeding pair disappeared, and presumably died, and the surviving members joined other groups, as breeders. It is likely that the proximate cause of the breakup of groups D and G was the death of a breeder, who could not be replaced by an adult from within the group.

Most of the changes in group membership were caused by recruitment of young by reproduction and death of group members rather than by intergroup movement. Of the 46 fully grown birds known to have been added to groups, 35 were offspring of the respective breeding pairs, and



Group:	A	B	C	D	E	F	G	H	I	J	K	L
1974												
Adults	2	3	2	2		2						
2-year olds	0	0	1	0		0						
Yearlings	0	1	0	0		0						
Total	2	4	3	2		2						
1975												
Adults	2	2	2		3	2	3	2				
2-year olds	0	1	0		0	0	0	0				
Yearlings	1	2	0		1	0	2	2				
Total	3	5	2		4	2	5	4				
1976												
Adults	3	2 (x)	2		2	3 (x)		3 (x)	3	2		
2-year olds	0	2	0		0	0		1	0	1		
Yearlings	1	1	1		0	2		0	0	1		
Total	4	5	3		2	5		4	3	4		
1977												
Adults	2	3	2		2	2		4	3	3	2	2
2-year olds	1	1	1		0	0		0	0	1	0	0
Yearlings	3	2	2		2	0		0	1	1	2	1
Total	6	6	5		4	2		4	4	5	4	3
1978												
Adults		2	3 (x)		2					3	1	2
2-year olds		2	0		1					0	1	1
Yearlings		2	0		1					2	1	2
Total		6	3		4					5	3	5

FIG. 1. Composition of Beechey Jay breeding-season groups, 1974–1978. Each arrow indicates change in group membership of an individual bird; (x) indicates the immigration of a bird from an unknown source. Two fledglings (fl) from group G in 1975 emigrated to groups C and F, respectively.

only 11 immigrated. Of 84 birds that disappeared from their groups, 75 disappeared permanently from the study and only seven joined other known groups (see Fig 1, Appendix). The remaining two were observed subsequently on the study area but their group affiliation remained uncertain.

Three of the seven switches between known groups were by adult males, one of which (OO) switched once (group D to group C, 1974–1975), the other of which (OB) switched twice (group G to group F, 1975–1976, then to group L in 1978). One was by an adult female, AA, (B–E, 1974–1975); one by a 2-year-old (OA), sex unknown (C, 1974–A, 1976); and two by fledglings, one a male, RV, (G–C), the other of unknown sex, VG, (G–F).

All four of the birds that immigrated from unknown sources (indicated

TABLE 1

RELATIONSHIP BETWEEN HELPERS AND MEMBERS OF BREEDING PAIRS

		No. birds helping breeding pairs				
Year	Total helpers	Both parents	One parent	Probable parents[a]	Only non-parents	Birds of unknown relation
1976	14	2	5	3	2	2
1977	23	12	2	6	1	2
1978	14	4	6	2	0	2
Total	51	18	13	11	3	6

[a] Includes only birds banded as yearlings in groups with no known past history; birds banded as 2-year-olds or as adults in groups with no known past history were placed in the unknown relation category.

by (x) in Fig. 1) were adults, two females and two of unknown sex. One of the females (O/Wr) was a breeder in her first year after immigration; the other (RG) became a breeder after helping for 1 year. The other two (XX group C and P/B) were helpers for 1 and 2 years, respectively. In summary, adults of both sexes predominated among individuals known to have moved to different groups (8 of 11). Five of such adults were breeders in their first appearance in the new group but three were helpers.

Of eight instances in which one of the breeders disappeared and was replaced, the replacements were immigrants in four (O/Wr, OO, and OB twice). In two cases, the replacement was a bird that had immigrated previously: RG as an adult the year before and RV as a bird-of-the-year 2 years before. In the seventh instance, replacement was by a group member (see account of history of PV below). In the final case, replacement was by an adult (XX group E) that served as an adult helper in the previous year, but for whom we have no juvenile history.

Although parent-helper kinship was uncertain or altogether unknown in a number of instances, most helpers definitely were associated with at least one parent when protecting and feeding younger siblings or half-siblings (Table 1). But three definitely contributed to the rearing of less closely related individuals.

We found only one case of mating of close relatives; in 1978 PV mated with her presumed father, WV. PV was banded as a yearling in 1975 when she was a member of group B in which WV was the male breeder (Appendix). She was presumably one of the surviving members of a group of nestlings from a nesting attempt still in progress at the conclusion of our field work in 1974; WV was the male parent in that attempt.

Attentiveness.—On the average, some jay visited the nest to feed the nestlings once every 18 min (1374 visits in 405 h of observation). Breeding

TABLE 2

FEEDING VISITS BY AGE CLASS, SEX, AND ROLE

Age class	Sex	Role	$\bar{x}$ % of visits	$\bar{x}$ visits/h
Adult	female	breeder	24	0.84
Adult	male	breeder	35	1.24
Adult	female	helper	4	0.58
Adult	male	helper	1	0.50
2-year-old	?	helper	8	0.52
Yearling	?	helper	28	0.84

males accounted for the majority of the feeding visits, followed by breeding females and yearling helpers, and then by other classes (Table 2). The percentage of the feeding visits made by the breeders decreased as the number of helpers increased (Fig. 2; Fig. 3, groups B and E). Proportional contributions of breeding males varied more, both among years and among groups, than did those of breeding females. Although in groups consisting of only two or three, breeding males accounted for the majority of the feeding visits (Fig. 3, groups E, D, C, A), such males appeared to benefit most by the presence of yearling helpers (Fig. 3, groups B and E).

Individual birds did not account for an increased percentage of the feedings as they matured. Individuals made fewer feeding visits as 2-year-olds than they did as yearlings; birds helping as adults made no more visits than they had as 2-year-olds.

A multiple regression analysis, using dummy variables and the improvement concept (Draper and Smith 1966), was used to test for relation between variation in number of feeding visits per hour and (1) age of nestlings, (2) number of nestlings, and (3) number of feeders. Whereas both age and number of nestlings showed little relationship with feeding rate, the regression coefficient associated with number of feeders was significant at the 0.03 level ($F = 4.92$, df = 1, 37). A similar, but more extensive, regression analysis by Brown et al. (1978) on Grey-crowned Babblers (*Pomatostomus temporalis*) showed that metabolic demands of the nestlings and environmental factors had a greater effect on feeding rates than did the number of helpers. The same could be true for Beechey Jays.

All members of each group also assisted in defending nestlings and fledglings and defending the territory from other groups. The manner in which the vicinity of the nest (within about 10–15 m) was patrolled apparently depended upon group size. The five birds of one group were

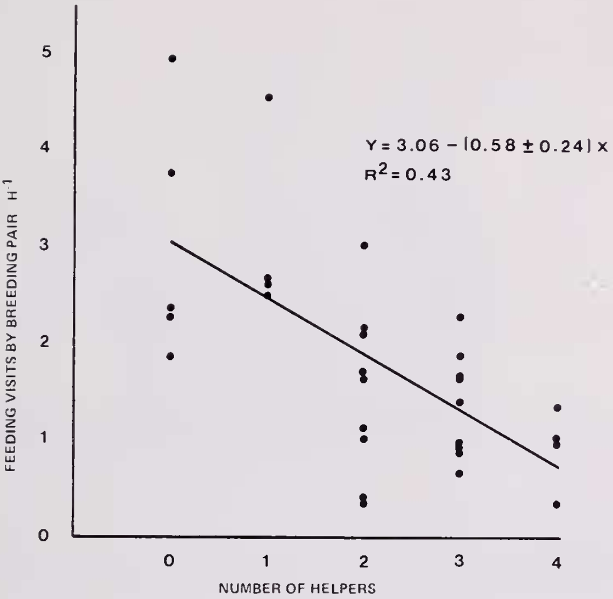


FIG. 2. Relationship between feeding rates by members of breeding pairs of Beechey Jays and the numbers of helpers. The value 0.24 is the 95% confidence interval for the estimate of the slope (−0.58).

observed on various occasions to station themselves as follows: one bird was at each of the corners of a square centered on the nest, while the breeding female was on the nest. In a group made up of only a breeding pair, defense was different. When both birds were present, one positioned itself near the nest while the other moved about the vicinity, stopping at various points. If only one bird was present, it moved about, stopping briefly at numerous points. Regardless of group size or the manner by which they patrolled, at least one bird was almost always present near the nest.

Based on actual observations of predation and on strong circumstantial evidence, the most important nest predators were Mexican beaded lizards (*Heloderma horridum*), a variety of snakes, and Magpie-jays (*Calocitta colliei*). Predators of lesser importance included squirrels, hawks, owls, crows, and possibly jaguarundi cats (*Felis yagouaroundi*). Most predators were driven off by the cooperative mobbing efforts of all group members. Actual physical encounters were rare because most predators retreated from the mobbing birds. However, on at least two occasions jays dived

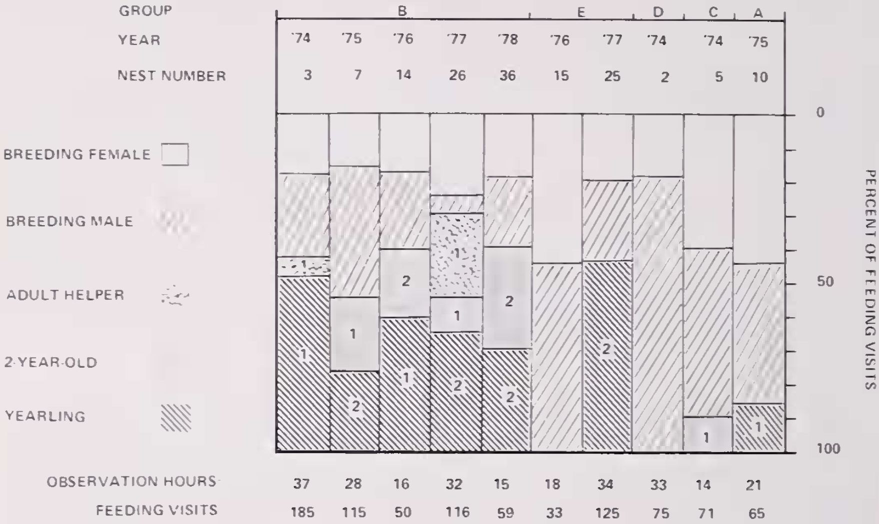


FIG. 3. Changes in percentage of feeding visits by age-class and role of members of Beechey Jay breeding season groups. Numbers within marked columns represent the number of helpers in that age-class in that year.

at squirrels and knocked them out of the nest tree. Jays also frequently mobbed human observers, mirrors used to observe nest contents, or mist nets when any of these were at or near the nest.

Unlike predators moving along the ground and perched birds of prey, avian predators on the wing were rarely mobbed; they were immediately, silently, and directly attacked and driven away. The extreme quickness with which avian predators could fly to a nest, seize a nestling, and fly off probably accounts for this different manner of attack.

Reproductive success.—Each group attempted only one nest at a time and did not nest again after successful fledging. An unsuccessful first nesting attempt was generally followed by a second attempt; no third attempts were observed. Clutch-size varied from three to five ($\bar{x} = 4.2$, N = 25) and the number of nestlings from one to five ($\bar{x} = 3.2$, N = 34). The mean number of fledglings produced per group per year was 2.3 (range: 0–5, N = 22); variation among years was remarkably low, with extremes of 2.0 and 2.5. Using Green's (1977) modification of Mayfield's (1961, 1975) method, we calculated 0.29 as the overall probability that any egg would produce a fledgling.

Of 99 eggs, 15 were lost prior to the end of incubation, 13 when entire clutches disappeared; two were single losses from different nests. As no egg losses were attributable to either storms or abandonment, all 15 were

TABLE 3

REPRODUCTIVE SUCCESS AS RELATED TO THE PRESENCE OF HELPERS

	Groups without helpers (N[a])	Groups with helpers (N)	P[b] t-test	P[c] Fisher's
$\bar{x}$ fledglings produced/nest	1.93 (7)	2.32 (27)	>0.25	=0.41
$\bar{x}$ yearlings produced/nest	0.96 (7)	1.35 (22)	≃0.10	=0.81
$\bar{x}$ fledglings surviving to 1 year of age/nest	1.19 (5)	1.84 (16)	≃0.06	=0.52

[a] Number of nests.

[b] Pooled t-test; $\sqrt{x + \frac{1}{2}}$ transformation was employed (see Sokal and Rohlf 1969, Woolfenden 1975).

[c] Fisher's exact probability test (see Romesburg et al. 1981).

presumably lost to predators. Only 63 of the 84 eggs present at the end of the incubation period actually hatched.

Of 101 nestlings whose fates were known, 40 died and 61 fledged. Of those that died, 25 were lost to predators and 7 died as a result of disease (including parasitism) and/or starvation; the cause of death for the remaining 8 was unknown. Late jay nests (young hatched after the wet season began) lost a significantly greater proportion of nestlings than did early nests (Chi-square = 10.8, df = 1, $P < 0.005$). We have no evidence, for early or late nests, of either nest abandonment or loss of nestlings as a direct result of inclement weather.

Winterstein and Raitt (1983) showed that heavy infestations of parasitic fly larvae could greatly retard nestling growth and development and ultimately be fatal; however, the presence of even large numbers of these subcutaneous parasites did not significantly affect survival to one year of age.

We performed a number of statistical analyses to determine whether reproductive success was related to number of helpers. Spearman rank correlation tests of numbers of helpers versus both numbers of fledglings produced ($r_S = 0.08$, N = 23, $P = 0.72$) and number of young surviving to yearling age ($r_S = 0.27$, N = 14, $P = 0.36$) indicated non-significant relationships. We also compared reproductive output of groups with helpers to that of groups without helpers. As a first step, we employed t-tests on transformed data (Woolfenden 1975); the results (Table 3) indicated a possible significant difference in the number of fledglings surviving to the subsequent breeding season. However, our data (counts having only a narrow range of possible values) are more appropriately examined with a Fisher's exact probability test for $r \times c$ contingency tables (Sokal and Rohlf 1969; Romesburg et al. 1981). (This test, because of the excessive computations required, was not feasible for earlier workers prior to recent development of computer programs.) Results (Table 3) indicate that we

TABLE 4
SURVIVAL RATES FOR DIFFERENT AGE CLASSES OF BEECHEY JAYS

Age at start (years)	No. individuals at risk	No. survivors after 1 year	% survival rate
Fledgling	55	21	38
1	29	14	48
2	10	6	60
3+	73	51	70

have no grounds for rejecting the null hypothesis of no difference in reproductive output between the two sets of groups.

Survival.—We estimated survival rates from the histories of marked birds (Table 4). The apparent trend of increasing survival rate with age was confirmed by Chi-square tests. A survivorship curve based on the rates shown indicated that the expected longevity of a cohort of fledglings of a given breeding season is approximately 10 years. Although data on survival of older age classes are meager, of 11 adults marked in 1974—when they were at least 3 years old—three survived to 1978, when they were no younger than 7 years.

We emphasize that the survival rates of Table 4 are minimum estimates, based on birds known to be alive; other individuals of the various cohorts may have survived after moving out of the study area, although each year we searched unsuccessfully for marked birds in adjacent habitats. A concrete indication that the estimates are low is that they require that each breeding group, on the average, produce approximately six fledglings per year in order to replace the number of adults dying per year. In fact the actual average production of fledglings per group per year was 2.3, little more than one-third of what would be expected. As pointed out above, Fig. 1 indicates a low rate of immigration into the population and thus immigration is unlikely to have accounted for the disparity between measured production and estimated survival.

Not only are the estimates probably lower than the actual survival rates, but the latter might also be atypically low. A substantial proportion of the individuals that disappeared—and were presumed to have died—did so when their groups dissolved after clearing of their habitat. Such dissolution probably resulted in increased rates of mortality and/or emigration.

Stable groups with long known histories probably yield more typical and perhaps more accurate estimates of survival rates. Groups A, B, C, E, and F were such groups (Fig. 1). From them, over the years of the study, eight adults disappeared, presumed dead, yielding an estimated minimal survival rate of over 79%, as opposed to the estimate of 70% given in Table 4.

DISCUSSION

The principal objective of this study was to answer some fundamental questions concerning the mode of evolution of cooperative breeding in birds. What are the advantages and disadvantages of the helping system to the breeders? To the helpers themselves? Do the interests of parents and helpers coincide? Are they opposed? Are advantages direct? Or are they indirect, involving primarily benefits to kin?

Costs and benefits to breeders.—Positive correlation between presence of helpers and reproductive output is the principal direct benefit to breeding pairs shown in a number of other cooperative species (Florida Scrub Jay, Woolfenden 1975; and others cited in a review by Brown 1978; see also recent experimental evidence of Brown et al. 1982). In the absence of such correlation in this study, we cannot conclude that helpers in Beechey Jays confer an immediate reproductive advantage on the breeding pairs. It is possible, however, that such an advantage could be demonstrated with a larger sample, especially of breeding pairs that had no helpers.

Another potential benefit to the breeding pairs is that, by their efforts at nest building and feeding and protecting young, helpers might have contributed to the survival and thus to the residual reproductive value and lifetime fitness of the breeders. Pertinent to this possibility is the relationship between number of helpers and feeding rate of parents. For each additional helper, the breeders made, on the average, one less visit each 2 hours. Presumably, the lower parental feeding rates result in a substantial saving of time and energy, and lower the risk of predation.

Helpers also participated actively in defense of nests and fledglings against predators, and again it is logical to presume that their assumption of a portion of the risks inherent in such defense reduced risks to members of the breeding pair. Whether these apparent benefits to the breeders did in fact increase their survival and overall reproductive value can only be inferred in the absence of adequate data on survival in relation to number of helpers. It has been shown that Florida Scrub Jay breeders with helpers do indeed survive longer than those without helpers (Stallcup and Woolfenden 1978).

The presence of helpers on the territory has been viewed by others (e.g., Brown 1974; Gaston 1978; Ligon 1981; Emlen 1982a, b) as a form of extended parental care. As most helpers are offspring of the breeders, benefits derived by the helpers (see below) inevitably provide an additional increment to the fitness of the breeders.

Costs to the Beechey Jay breeders of the helping system appear minimal, in contrast to the situation described by Zahavi (1974) among others. Helpers consistently behaved inconspicuously in the vicinity of the nest—except when mobbing—and were indistinguishable in this behavior from breeders. Had helpers been a serious liability to breeders, we might have expected to see aggression toward them by the breeders (Emlen 1982b), but no such agonism was evident. Any cost to the breeders of the use by helpers of the resources of the territory were at least partially offset by helper participation in territorial defense.

Costs and benefits to helpers.—A full discussion of the costs and benefits to helpers requires a consideration of those entailed first, in remaining on the natal territory and second, in behaving as a helper (Brown 1978, Emlen 1982b). The obvious primary cost of staying and helping is that of foregoing breeding and expending time, energy, and risk of predation to rear young that are usually less closely related to them than their own offspring would be (Brown 1974, Koenig and Pitelka 1981, Emlen 1982a, and many others). Partly offsetting this cost is the substantial probability that the young helper will itself eventually breed. This probability is a consequence of the survival rates and the dynamics of the groups. First, it can be calculated readily from the survival rates of Table 4 that a yearling helper has at least a 29% probability of reaching adulthood (at least three years of age). Once a bird reaches that age the probability that it will breed is high. There is a 30% chance that, in its group in any given year, at least one member of the previous year's breeding pair will have disappeared. Furthermore, the probability that an adult will have an opportunity to breed is increased by the possibility of emigrating to a neighboring group in which such an opening has occurred; as shown, birds move rather freely between groups to fill such openings. The overall probability of an adult having an opportunity to breed is illustrated by the fact that 85% (29 of 34) of all known individual adults were breeders in at least one season. Only one adult was known to have died before having bred; the other four non-breeders were still alive at the end of the study and may eventually have bred. It is also relevant that two known birds bred in a minimum of five consecutive seasons and 11 more bred in at least three seasons. Of the remaining 16 birds, two were known to have bred in only 2 years, the remaining 14 were either breeders when the study started or when it ended and probably bred in more than the one or two seasons we recorded. Clearly, birds that survived to become breeders enjoyed a substantial reproductive value.

A more important factor mitigating the presumed cost of foregoing breeding by the young helper is the low probability that it would be able to breed successfully should it leave its natal territory and attempt to nest elsewhere. The choices faced by such a youthful member of a cooperatively breeding species were discussed first by Selander (1964) and Brown (1969) and recently by Koenig and Pitelka (1981) and Emlen (1982a). Unlike some cooperative breeders, Beechey Jays do not appear to have highly specific habitat requirements and the extent of their habitat, although shrinking (Raitt and Hardy 1979), was not historically highly limited. Nevertheless, observations on our study area and elsewhere within the range of the species indicate that virtually all obviously favorable habitat (see Raitt and Hardy 1979 for habitat description), and some apparently less favorable, is included in permanent territories defended by established breeders, usually with helpers. As pointed out by Selander (1964), Brown (1969), Koenig and Pitelka (1981), Emlen (1982a), and many others, in such a situation a young individual would find it nearly impossible to establish a territory on which to breed. In the case of Beechey Jays, whose habitat in the later half of the nonbreeding season is very dry and low in available food (Raitt and Hardy 1979), it may well be that survival in marginal habitats between breeding seasons is as critical as the problem of finding habitat in which to attempt breeding. Thus the principal benefit to the nonbreeding Beechey Jay of remaining on the territory appears to be that attributed to helpers of other species of birds by Woolfenden (1975, 1981), Woolfenden and Fitzpatrick (1978), Brown (1978), Ligon and Ligon (1978a, b), Ligon (1981) and Emlen (1981) among others; this is that helpers are able to share in the resources of a territory in suitable habitat, defended by a group, until they obtain an opportunity to breed. Supplementary benefits to remaining on the territory are those of membership in a group: cooperation in locating aggregated food sources, warning of and mobbing predators, and defense of the territory (but see Alexander 1974 for discussion of disadvantages of living in a group).

If benefits to the helper of remaining on a territory in which it is not a breeder are relatively clear, benefits obtained by helping behavior (i.e., building the nest, feeding of young, guarding the nest and fledglings, and territorial defense) are less clear. Benefits of helping in two well studied species apparently depend on the manner in which helpers ascend to breeding status. In Florida Scrub Jays nonbreeders may gain their own breeding territory through helping (Woolfenden and Fitzpatrick 1978). Most female helpers that become breeders disperse to other groups to join mature, unmated males. Males on the other hand remain on their natal territories longer than females (and provide more assistance in each season of helping). Most mature male helpers become breeders through obtaining as their own territory a portion of their natal territory and mating with an immigrating adult female. This "budding" of new territories is made possible by expansion of the original territory as the group increases in size. Thus helpers are envisioned as helping to create their own opportunity to breed by their contribution to the expansion of their natal territory. Although we are hindered in comparing the above system with that in the Beechey Jay by paucity of data on sexual identity, several attributes of the Scrub Jay system are not apparent in that of the Beechey Jay. We did not find a trend of expansion of territories with group size for groups that we knew well. Group A enlarged progressively from 2 to 6 (Fig. 1, Appendix) in a series of years without discernible change in its territory. Group B's territory, with which we were most familiar, underwent some slight changes in size that were not correlated with changes in the size of the group. Concomitantly, we saw no evidence of budding of new territories from old ones.

No instances occurred of a single bird leaving one group to join another single bird of the opposite sex to form a new group. Of helpers that became breeders, female PV remained in her natal group, male RV moved from group G to group C as a yearling and then bred as a 3-year-old, female AA was an adult helper with group B in 1974 and became a breeder in group E in 1975, and female RG immigrated to become an adult helper with group F in 1976 and then a breeder with that group the following year. Thus, two female helpers moved to other groups before breeding, but one male did likewise, and one female remained in her natal group. The sample is small but the behavior of the birds did not conform to the pattern found among Florida Scrub Jays. The histories of two adult male breeders (OO and OB) also failed to conform. The mate of each disappeared (died?) between breeding seasons and each became a breeder in a different group in which the breeding male had disappeared. If the system in Beechey Jays were as in Florida Scrub Jays, these males would have remained on their territories to be mated to dispersing adult female helpers from some other group.

The Green Woodhoopoe (*Phoeniculus purpureus*) also possesses a well-studied, rather elaborate system of dispersal of helpers to become breeders (Ligon and Ligon 1978a, b; Ligon 1981, 1983). Unlike communal jays that have been studied, woodhoopoes apparently suffer high mortality rates and social groups are in a greater state of flux, with new ones being formed rather frequently. Apparently the usual manner of ascendancy of an adult helper to breeding status is for one to disperse along with younger flock mates of the same sex, whom it had helped to rear. "Older helpers clearly gain by helping to produce younger flock mates in that the younger birds can be 'used' to obtain breeding status for the older (former) helper and . . . care for the older bird's own nestlings." (Ligon 1981:242). The only behavior resembling this that we saw was the dispersal of breeder OB with one of his offspring to group F. No other dispersing Beechey Jay was accompanied by another group member.

In summary, Beechey Jay helpers become breeders either by dispersing to another group or remaining in their natal group but there seems to be no consistent difference between the sexes. The territorial and dispersal behavior of Beechey Jays appears not to be such that helpers increase the probability of becoming breeders by helping to enlarge their territories nor such that they increase the probability that they will have younger sibling helpers to accompany them in dispersal.

Parenthetically, the dispersal pattern seems to contain no particular mechanism that would prevent incest, and indeed the case of PV in group E was an apparent case of a daughter mated to her father. Furthermore, inbreeding may be the explanation of the unusually high proportion (25%) of eggs that failed to hatch in this study (see Koenig 1982).

Helpers may help at the nest in order to gain access to it or to the breeder of the opposite sex for reproductive purposes. Polygamous or promiscuous matings with members of the breeding pair by other group members of one or both sexes have been reported among several cooperatively breeding species, including Acorn Woodpeckers (Stacey 1979, Koenig and Pitelka 1981) and others cited by Emlen (1982b). Among the many studied cooperative jays, such behavior is reported only for the Brown Jay (*Cyanocorax morio*) (Lawton 1979), and Black-throated Magpie-jay (Winterstein, unpubl). We have no evidence of such plural breeding in Beechey Jays. Exceptionally large clutches or ones of heterogeneous appearance were not detected, which would appear to rule out polygyny or female promiscuity. Male helpers could have stolen copulations, but as mentioned previously, we saw no antagonism by breeders toward helpers, which would be expected should such copulations be at all frequent.

Another possibility is that nonbreeders increase their own later effectiveness as parents by helping. Unlike young Brown Jays (Lawton and Guindon 1981) and Florida Scrub Jays (Stallcup and Woolfenden 1978), young Beechey Jays did not increase their feeding rates as they became older, either within their first season as helpers or between that season and later ones. In the closely related southern San Blas Jays (*Cyanocorax s. sanblasiana*), however, in which some individuals less than 3 years old do become breeders, those individuals are less successful than are older breeders (Hardy et al. 1981), perhaps because of less experience as nest attendants. Feeding rate is surely an imperfect measure of potential effectiveness in breeding; without a better test than our data provide, we cannot draw a firm conclusion as to the possible advantage of experience in helping.

A more likely benefit that the helper gains from helping is that if it becomes a breeder in the same group, it may receive the help of younger birds that it had helped to rear (Brown 1978, Emlen 1982b). In some respects this benefit resembles that described for the Green Woodhoopoe, but it does not involve aid in obtaining breeding status. Four different Beechey Jays became breeders in the same territories in which they had been helpers. One of these (PV) was helped in producing three fledglings in the last year of the study by two yearlings and two 2-year-olds that it had helped to rear (see Appendix, group B). In the other three cases the potential helpers did not survive to the next breeding season to reciprocate when the older helper became a breeder. The fifth known helper that became a breeder did so by changing groups.

Another possible explanation for helping behavior is that it is "payment" (sensu Gaston 1978) for the opportunity to share the resources of the territory and to succeed to breeding status on it (Brown 1969, Koenig and Pitelka 1981). Breeders may not allow nonbreeders to remain on a territory if they do not help. We are compelled to admit that we have no direct evidence for this kind of behavior, but as is usual among cooperative breeders, all nonbreeding Beachey Jays did indeed help and no instance was observed that suggested a breeder's expelling a potential helper. Thus we offer this possibility in large part by default, because we have been forced to reject most other possible benefits of helping.

A final possible benefit of helping to the helper is indirect (sensu Brown 1980), via kin selection. Various students of cooperative breeding in birds have argued either for or against the importance of kin or indirect selection in the evolution of helping (see Brown 1978, 1980, in press; Brown and Brown 1981a, b; Brown et al. 1982; Koenig and Pitelka 1981; Ligon 1981, 1983; Woolfenden 1981), often without convincing tests of their respective hypotheses. While our findings likewise fail to provide such a test, most Beechey Jay helpers did help one or both parents (Table 1). Any resulting gain in the direct fitness of those parents inevitably produced an indirect benefit to the helpers.

CONCLUSIONS

We believe that the Beechey Jay helping system imposes little or no costs to breeders and that they probably gain benefits in increased survival. A larger sample size might also show an increase in annual breeding success. Inclusion of nearly all suitable habitat within territories defended the year around by breeders, usually with helpers, provides the advantage to young individuals of remaining on their home territory with their parents. This explanation has gained wide acceptance among students of cooperatively breeding birds. Our findings are consistent with three possible explanations for the adaptive advantage to helpers of helping: (1) that they help to rear young that later will become their helpers; (2) that helping is a "payment" to breeders for allowing helpers to remain on the territory; and (3) that the benefits to helpers are indirect. We cannot point to any one of these as more important than the others and believe that all three may be operative. The nature of our conclusions concerning costs/benefits precludes more than passing mention of recent discussions of such characteristics of avian cooperative breeding behavior in relation to general sociobiological theory, which feature conflicting terminology and conclusions (see Brown 1983, in press; Ligon 1983).

Social organization and behavior in Beechey Jays resemble those in Florida Scrub Jays in many respects: some pairs have helpers but some do not; territories are permanent, defended throughout the year; only one pair of adults per territory are breeders in any particular breeding season and a single nesting is the rule, unless the first attempt fails; helpers include all major age classes; and helpers are usually closely related to breeders. On the other hand, two major differences are evident. Unlike Florida Scrub Jays, Beechey Jay helpers do not greatly increase the annual reproductive success of the breeders that they help. And Beechey Jay helpers have a more loosely organized system of dispersal to become breeders, in contrast to the marked differences between sexes and territorial expansion and budding in Florida Scrub Jays. The principal conclusion to be drawn from these contrasts is that a successful system of cooperative breeding in jays need not involve marked increase in breeding success on the part of aided breeders or an elaborate system of eventual dispersal of helpers.

The similarities to Florida Scrub Jays stressed above are in contrast to the marked differences between Beechey Jay ecology and behavior and those of its close relative in the subgenus *Cissilopha.* Variation in the habitat among the forms of *Cissilopha* has been proposed as the explanation for the variation in social behavior (Raitt and Hardy 1979, Hardy et al. 1981). The highly social Southern San Blas Jay occupies habitats that are severely altered by humans and rich in food, whereas the least social Beechey Jay is found in more natural and less productive areas. The other forms of *Cissilopha* are intermediate in both social system and habitat. Variation in habitat also may be related to the differences in dispersal pattern between Beechey Jays and Florida Scrub Jays and Green Woodhoopoes: somewhat elaborate systems of territory budding and group dispersal may require habitat that is more open than that of Beechey Jays.

The dense forest of that habitat may preclude sufficiently close monitoring of adjacent groups.

SUMMARY

Structure and dynamics of breeding groups in the cooperatively breeding Beechey Jay (*Cyanocorax beecheii*) were studied near Mazatlan, Mexico, from 1974–1978. Breeding groups were composed of one breeding adult member of each sex and 0–4 helpers, which varied in age from yearling to adult (3 years or older). Most groups were relatively stable in membership and occupied the same territories throughout our study. A few groups dissolved, most when habitat of their territory was destroyed. Adults predominated among birds moving from one group to another; neither sex predominated. Breeders that disappeared were replaced more often by immigrants than by group members.

All group members assisted in feeding and defending nests, fledglings, and territories. Most helpers were offspring of one or both breeders. Male breeders accounted for the majority of the feeding visits, followed by female breeders and yearling helpers. Individual birds did not account for an increased percentage of feeding visits as they matured. A group attempted no more than one successful nesting and produced an average of 2.3 fledglings per year. Major losses of eggs were through predation (15 of 99) and infertility (21 of 84). Predation was the principal source of nestling loss (25–33 of 40 lost, of 101 total). Groups with helpers did not realize an increase in annual reproductive success when compared to groups without helpers.

The probability of survival increased with age; adult annual survival rate was at least 70% and probably nearer to 80%. Only one known bird failed to breed after reaching adulthood and at least 29 of 34 adults became breeders.

Breeders incur few costs in allowing helpers to remain on the territory and assist at the nest. They probably benefit from the presence of helpers through increased survival and thus in lifetime reproductive output. Helpers forego breeding and remain on occupied territories because by doing so they have a greater opportunity to survive and ultimately reproduce than if they dispersed into ecologically unsuitable, unoccupied areas. Likely reasons that helpers help are that such behavior (1) is a form of payment to the breeders for allowing them access to territorial resources, (2) results in the gain of future help of the young they help raise, and (3) increases their indirect fitness because they help close kin. Any combination of these reasons may be operative.

The social organization and demography of Beechey Jays are remarkably similar to those of Florida Scrub Jays but we found no evidence of the territorial expansion and budding characteristic of Florida Scrub Jays or of specialized dispersal mechanisms as in that species and Green Woodhoopoes. These differences may be related to differences in habitat. Similarly, variation in habitat seems to underlie the considerable differences in social organization between the Beechey Jay and its relatives in *Cissilopha.*

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DEPT. BIOLOGY, NEW MEXICO STATE UNIV., LAS CRUCES, NEW MEXICO 88003 (RJR AND SRW) AND FLORIDA STATE MUSEUM, UNIV. FLORIDA, GAINESVILLE, FLORIDA 32611 (JWH). (PRESENT ADDRESS SRW: DEPT. STATISTICS, NORTH CAROLINA STATE UNIV., RALEIGH, NORTH CAROLINA 27650.) ACCEPTED 7 MAR. 1984.

APPENDIX

HISTORIES OF BEECHEY JAY NESTING GROUPS FROM 1974–1978[a]

Group	Bird (sex)	1974	1975	1976	1977	1978
A	WO (♂)	X, Ad, Np	B, NP	NP	NP	1[b]
	VR (♀)	X, Ad, NP	B, NP	NP	NP	–
	AB	–	B, Yr, H	–	–	–
	GA	–	B, Fl	H	H	–
	BA	–	–	B, Fl	H	–
	GR	–	–	B, Fl	H	–
	VP	–	–	B, Fl	H	–
	OA	–	–	2, H	–	–
B	WV (♂)	B, Ad, NP	NP	NP	NP	NP
	PP (♀)	B, Ad, NP	NP	–	–	–
	AA (♀)	B, Ad, H	3	–	–	–
	GG	B, Yr, H	H	–	–	–
	OG	–	B, Yr, H	H	–	–
	PV (♀)	–	B, Yr, H	H	H	NP
	GV	–	B, Fl	H	H	–
	O/WR (♀)	–	–	X, Ad, NP	B, NP	–
	O/Ar	–	–	–	B, Yr, H	H
	XX	–	–	–	Yr, H	H
	G/Rr	–	–	–	B, Fl	H
	G/Or	–	–	–	B, Fl	H
C	VV (♂)	B, Ad, NP	–	–	–	–
	BR (♀)	B, Ad, NP	NP	NP	NP	NP
	OA	B, 2y, H	2	–	–	–
	OO (♂)	–	4, NP	NP	NP	–
	AV	–	–	B, Fl	H	–
	RV (♂)	–	–	5, H	H	NP
	XX	–	–	–	Yr, H	–
	XX	–	–	–	–	Ad, H
D	OO (♂)	B, Ad, NP	4	–	–	–
	WW (♀)	B, Ad, NP	–	–	–	–
E	RR (♂)	–	X, Ad, NP	B, NP	NP	NP
	AA (♀)	–	3, NP	–	–	–
	XX (♀)	–	Ad, H	NP	NP	NP
	XX	–	Yr, H	–	–	–
	BG	–	–	B, Fl	H	–
	PB	–	–	B, Fl	H	H
	A/Gr	–	–	–	B, Fl	H
F	GB (♂)	X, Ad, NP	B, NP	–	–	–
	OP (♀)	B, Ad, NP	NP	NP	–	–
	WA	–	B, Fl	H	–	–
	RG (♀)	–	–	B, Ad, H	NP	–
	OB (♂)	–	–	6, NP	NP	7
	VG	–	–	8, H	–	–

APPENDIX
CONTINUED.

Group	Bird (sex)	1974	1975	1976	1977	1978
G	OB (♂)	—	B, Ad, NP	6	—	—
	AP (♀)	—	B, Ad, NP	—	—	—
	XX	—	Ad, H	—	—	—
	XX	—	Yr, H	—	—	—
	XX	—	Yr, H	—	—	—
	RV (♂)	—	B, Fl	5	—	—
	VG	—	B, Fl	8	—	—
H	GO (♂)	—	B, Ad, NP	NP	NP	—
	GV (♀)	—	X, Ad, NP	B, NP	NP	—
	VA	—	B, Yr, H	H	H	—
	XX	—	Yr, H	—	—	—
	P/B	—	—	B, Ad, H	H	—
I	AW (♂)	—	—	B, Ad, NP	NP	—
	XX (♀)	—	—	Ad, NP	NP	—
	RA (♂)	—	—	B, Ad, H	H	—
	AO	—	—	B, Fl	H	1
J	XX (♂)	—	—	Ad, NP	NP	NP
	OW (♀)	—	—	B, Ad, NP	NP	NP
	AR (♂)	—	—	B, 2y, H	H	H
	XX	—	—	Yr, H	H	—
	VW	—	—	B, Fl	H	—
	V/Or	—	—	—	B, Fl	H
	G/Wr	—	—	—	B, Fl	H
K	XX	—	—	—	Ad, NP	9
	V/Gl	—	—	—	B, Ad, NP	—
	XX	—	—	—	Yr, H	—
	A/Gl	—	—	—	B, Yr, H	9
	W/Vl	—	—	—	B, Fl	9
L	XX	—	—	—	Ad, NP	—
	XX (♀)	—	—	—	Ad, NP	NP
	B/Pl	—	—	—	B, Yr, H	H
	W/Bl	—	—	—	B, Fl	H
	G/Al	—	—	—	B, Fl	H
	OB (♂)	—	—	—	—	7, NP

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[a] Birds are originally listed in the group and year in which they first appeared. — indicates that the bird disappeared and was presumed dead, fledglings that failed to survive to at least one-year-of-age are not included; X—unbanded, presumed to be the same bird banded in a subsequent year; B—banded; Ad—adult (≥3 years of age); 2y—two-year-old; Yr—yearling; Fl—fledgling; NP—member of nucleus pair (= breeder); H—helper.

[b] Numbers indicate as follows: 1—Observed on study site, but group had dissolved; 2—Absent from study site in 1975, appeared in group A (from group C) in 1976; 3—Moved to group E, from group B, 4—Moved to group C, from group D; 5—Moved to group C, from group G; 6—Moved to group F, from group G; 7—Moved to group L, from group F; 8—Moved to group F, from group G; 9—No nest found, but group presumed present and active on study site.